# The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae)

# GIORGIO CARNEVALE\*

CNR - Istituto di Geoscienze e Georisorse, c/o Dipartimento di Scienze della Terra, via S. Maria, 53, I-56126 Pisa, Italy

#### (Received 13 May 2003; accepted 26 April 2004)

**Abstract** – The first fossil ribbonfish, *Trachipterus mauritanicus* sp. nov., based on a single specimen, is described from Sidi-Brahim, an Upper Miocene (Messinian) locality situated in the central sector of the Chelif Basin, northwestern Algeria. *Trachipterus mauritanicus* sp. nov. is characterized by a flattened neurocranium and an advanced insertion of the dorsal fin. Based on skeletal morphology, *T. mauritanicus* sp. nov. appears to be related to *T. arawatae* and *T. trachypterus. Trachipterus mauritanicus* sp. nov. represents the eighth taxon described up to now from Sidi-Brahim. The occurrence of the first fossil member of the family Trachipteridae from the Upper Miocene sediments of northwestern Algeria emphasizes the crucial importance of the Messinian ichthyofaunas from Algeria to our knowledge of the fossil record of the Teleostei.

Keywords: Teleostei, Lampridiformes, Trachipterus mauritanicus sp. nov., Miocene, Algeria.

## 1. Introduction

The Lampridiformes are a group of exclusively marine fishes with a poor fossil record dating from to Late Cretaceous. They consist 12 living genera included in seven families. All living lampridiforms are coastal or pelagic in temperate and tropical seas. This group is characterized by an extreme morphological disparity, and it includes some of the most bizarre vertebrate species. One of the most peculiar representative of the order is the oarfish, Regalecus glesne, which can reach more than 15 meters in length, and was considered in ancient times as the legendary sea serpent (Fitch & Lavenberg, 1968). Because of their wide morphological differences, lampridiforms were not recognized as a natural group until the pioneering work of C. Tate Regan (1907), who provided the first comprehensive taxonomic analysis of this group and named these fishes Allotriognathi. Regan (1907) divided the lampridiforms into two groups: the Bathysomi, which included the families Lamprididae (= Selenichthyes) and Veliferidae (= Histichthyes), and the Taeniosomi, the elongate lampridiforms, which consisted of the Lophotidae and the Trachipteridae. Later, Regan (1924) added the Stylephoridae to the group. The term Lampridiformes was introduced by Greenwood et al. (1966). The monophyly of this group has been corroborated by a cladistic analysis of morphological (Olney, Johnson & Baldwin, 1993) and molecular (Wiley, Johnson & Dimmick, 1998) data. Several hypotheses have been presented on the phylogenetic position of lampridiforms within teleosts. Stiassny & Moore

(1992) proposed two alternative scenarios, placing Lampridiformes as either basal acanthomorphs or basal percomorphs. The first hypothesis was supported by Olney, Johnson & Baldwin (1993) and Johnson & Patterson (1993), who considered them as the sister group of the Euacanthomorpha. In contrast, recent studies of evolutionary genomics (Miya, Kawaguchi & Nishida, 2001; Miya *et al.*, 2003) concluded that the Lampridiformes are not acanthomorphs but ctenosquamates, and placed this group as the sister taxon of Ateleopodiformes.

Regan's Trachipteridae comprised two genera, Trachipterus and Regalecus. A revision of this family by Walters & Fitch (1960) placed Regalecus in the separate family Regalecidae, and erected two new trachipterid genera: Desmodema and Zu. These fishes are characterized by unique morphological features, such as ribbon-like body form (Oelschläger, 1976), specialized integument (Walters, 1963), and rotating eye (Haedrich, 1974). The systematics of trachipterids at the specific level are somewhat confused (see, e.g., Rosenblatt & Butler, 1977; Heemstra & Kannemeyer, 1984; Olney, 1984). To date, ten living species are recognized, and no fossil taxa have been known. The purpose of this paper is to describe the first fossil representative of the family Trachipteridae. The fossil was recently found among the undescribed material of the paleoichthyological collection of the Muséum National d'Histoire Naturelle in Paris.

## 2. Locality and stratigraphy

The material was collected in the 1920's from a sedimentary succession croppingout near Sidi-Brahim,

<sup>\*</sup> E-mail: carnevale@dst.unipi.it



Figure 1. Type locality of *Trachipterus mauritanicus* nov. sp. The asterisk indicates the location of Sidi-Brahim.

in the central sector of the Chelif Basin, northwestern Algeria (Fig. 1). The outcrop is located near the Ouadi Bechela, several kilometres from the town of Mostaganem. The succession is affected by a moderate tectonization. Arambourg (1927) provided a schematic representation of the stratigraphy of the section. Unfortunately, he did not indicate the exact thickness of the different lithologies. A stratigraphic section is here restored based on the description of Arambourg (1927). The base of the section is represented by a great thickness of the so-called Globigerina marls. The marls are overlained by several meters of marly limestone, siliceous marls, and at least three tripolaceous intervals. Gypsum strata lie over the Tripoli. Pliocene sediments represent the upper part of the section.

The material comes from the Tripoli intervals. From a lithological point of view, the Tripoli consists of diatomites and diatomitic marls that are present in most of the Mediterranean domains. Nearly all of the stratigraphic section dates back to the Upper Miocene, Messinian (Arambourg, 1927). In Algeria, diatomitic deposits appear in coincidence with the occurrence of the Messinian biostratigraphic markers Globorotalia mediterranea/Globorotalia conomiozea (Poignant & Moisette, 1992; Mansour et al., 1994), which was dated 7.12 Ma by Krijgsman et al. (1995). Moreover, the onset of evaporite sedimentation in the Mediterranean was fixed at 5.96 Ma by Krijgsman et al. (1999; 2001). Thus, because of the stratigraphic position of the fossiliferous layers, which are located below the gypsum strata, the fossil fishes of Sidi-Brahim are approximatively 6 million years old.

#### G. CARNEVALE

#### 3. Methods

The type and only known specimen is deposited in the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle (MNHN), Paris (MNHN ORA1221). The specimen was examined using a stereomicroscope equipped with a *camera lucida*. Measurements were taken with a dial caliper, to the nearest 0.1 mm. Comparative data were derived mainly from the literature.

# 4. Systematic palaeontology

Subdivision TELEOSTEI sensu Patterson & Rosen, 1977 Order LAMPRIDIFORMES sensu Olney, Johnson & Baldwin, 1993 Family TRACHIPTERIDAE sensu Walters & Fitch, 1960 Genus Trachipterus Goüan, 1770

Trachipterus mauritanicus sp. nov.

*Diagnosis*. A *Trachipterus* that differs from all other species of the genus by a more advanced insertion of the dorsal fin and by a more flattened dorsal portion of the neurocranium.

*Holotype*. MNHN ORA1221, a completely articulated skull and the anterior part of the dorsal fin, preserved on diatomite.

*Horizon and locality*. Upper Miocene (Messinian) of Sidi-Brahim, central portion of the Chelif Basin, northwestern Algeria.

*Derivation of name*. From Mauritania Caesariensis (Latin), the ancient name of the North Africa region that includes the type locality.

# 4.a. Description (Figs 2-6; 8a)

Laterally compressed teleost. Head length 34.3 mm. Other measurements as percentage of head length: head depth (66.7 %), snout length (32.9 %), orbit (21.5 %), eyeball (based on preserved pigment) (17.7 %).

The neurocranium is moderately deep posteriorly, and becomes deeper in the posterior part of the frontal region and shallower anteriorly. The orbit is large, about equal to half the length of the neurocranium. The eyeball is large and preserved as a thin carbon film. The bones are delicate, feebly ossified. The frontals are the largest bones on the neurocranium. The anterior portion of these bones represents the lateral wall of a cradle-like chamber. The two contralateral frontals probably do not meet at the midline anteriorly, as in other trachipterids. The frontal cradle walls end dorsally forming a prominent process. A welldeveloped crest is visible along the entire base of the frontal cradle. Two additional frontal ridges are clearly recognizable on the lateral surface of the frontal cradle. All these ridges arise from a prominent



Figure 2. *Trachipterus mauritanicus* nov. sp. from the Miocene of Algeria. Holotype, MNHN ORA1221, left side, lateral view. Scale bar 20 mm. Photograph courtesy of Daniel Goujet.

central frontal ridge, which continues posteriorly on the sphenotic and the pterotic. The frontals are posteriorly sutured to the supraoccipital, the parietal and the sphenotic. The parietals are separated at the midline by the supraoccipital and the epioccipitals. The suture between the supraoccipital and the epioccipitals is difficult to interpret. The anteriormost part of the neurocranium is obscured by the overlying maxilla, and the morphology of the vomer cannot be observed. The lateral ethmoids are anterior to the mesethmoid and are sutured dorsally to it and to the frontals. The mesethmoid, orbitosphenoid and pterosphenoid form the dorsal margin of the orbit. The basisphenoid is well preserved, but partially displaced. The sphenotic, prootic, and basioccipital are recognizable in the posterior part of the neurocranium. The parasphenoid is long and slender. Posteriorly it attaches to the ventral part of the basioccipitals. The nasal is preserved in life position, immediately anterior to the frontal. Of the infraorbital bones, the lachrymal is preserved. This bone is laminar, subrectangular and bears a thin process ventrally. The mouth is small. The upper jaw presumably is highly protrusible. The premaxilla is

a large bone with an extremely elongate ascending process. A large rostral cartilage inserting into the frontal cradle was probably located distally on the posterior margin of the ascending process of the premaxilla. Two recurved pointed premaxillary teeth are preserved. The alveolar process of the maxilla is globose, nearly ovoid in outline. It is ornamented with light radial grooves and ridges. There is a small ascending maxillary process. The mandible consists of the dentary and the angulo-articular. A single pointed tooth is visible anteriorly, along the dorsal margin of the dentary.

The suspensorium consists of the ectopterygoid, endopterygoid, hyomandibula, metapterygoid, quadrate, palatine and symplectic. The metapterygoid has a highly convex anterior margin. The endopterygoid is rather large. This bone bears a median ridge which passes anteriorly on the palatine and on ectopterygoid. The palatine prong is absent. The quadrate is subtriangular, fan-shaped. The symplectic is a cylindrical slender bone. The hyomandibula is elongate. It appears to articulate with the basioccipital, but this position could be due to the fossilization processes that caused



Figure 3. *Trachipterus mauritanicus* nov. sp., reconstruction of the skull, left side, lateral view. Abbreviations: aa, angulo-articular; bo, basioccipital; bsp, basisphenoid; d, dentary; ecp, ectopterygoid; enp, endopterygoid; epo, epioccipital; exo, exoccipital; fr, frontal; h, hyomandibula; iop, interopercle; l, lachrymal; le, lateral ethmoid; me, mesethmoid; mtp, metapterygoid; mx, maxilla; n, nasal; op, opercle; ors, orbitosphenoid; pa, parietal; pal, palatine; pas, parasphenoid; pmx, premaxilla; pop, preopercle; pro, prootic; pto, pterotic; pts, pterosphenoid; q, quadrate; soc, supraoccipital; sop, subopercle; spo, sphenotic; sym, symplectic.



Figure 4. *Trachipterus mauritanicus* nov. sp., reconstruction of the hyoid bar, left side, lateral view. Abbreviations: cha, anterior ceratohyal; chp, posterior ceratohyal; hyd, dorsal hypohyal; hyv, ventral hypohyal.

partial displacement of the suspensorium. In fact, an original articulation with the prootic is more probable.

The opercular bones are well preserved. They are characterized by robust radial ridges, alternated with thin laminae of bone. The dorsal margin of the opercle appears to be slightly scalloped. The preopercle and interopercle are very large. The hyoid bar is massive and subrectangular in outline (Fig. 4). There are no apparent sutures between the dorsal hypohyal, anterior ceratohyal and posterior ceratohyal, but this is probably the result of lack of preservation. There are six



Figure 5. *Trachipterus mauritanicus* nov. sp., dorsal fin (pennant), left side, lateral view.

branchiostegal rays. Fragments of the gill arch series, probably of ceratobranchials and epibranchials, are visible. These fragments bear slender pointed teeth.

The dorsal fin (Fig. 5) inserts at the level of the vertical through the midpoint of the orbit. Six rays of the fin pennant are preserved, with the pennant crest formed by the anteriormost dorsal rays.



Figure 6. Reconstruction of Trachipterus mauritanicus nov. sp.

Each of these rays bears small lateral spinules. The distal parts of the dorsal-fin rays are not preserved, but they were probably well developed originally. The rays are supported by six pterygiophores. The anteriormost pterygiophore is greatly enlarged. The second pterygiophore is better developed relative to pterygiophores 3 to 6. The pterygiophores are inclined forward over the neurocranium. Although there are no preserved vertebrae, it is probable that the first pterygiophore inserted anterior to the first neural spine. Very little of the series of lateral line scales is preserved. A small stout pointed spine is visible on the slab. This spine is evidently displaced from its original position. Because of its morphology, this spine can be interpreted as the remnant of a lateral line scale (see, e.g. fig. 19 in Olney, Johnson & Baldwin, 1993).

## 4.b. Remarks

This new Miocene fossil can be unequivocally assigned to the Lampridiformes based on four synapomorphies (see Olney, Johnson & Baldwin, 1993): mesethmoid posterior to lateral ethmoids, elongate ascending process of the premaxilla that probably inserted into the frontal cradle, absence of palatine prong, and (presumed) insertion of the first dorsal-fin pterygiophore anterior to the first neural spine. The presence of the supraoccipital which separates the parietals, the orbitosphenoid which anteriorly contacts the mesethmoid, the (presumed) protrusibility of the mouth, and the presence of six branchiostegal rays also suggest its inclusion in the Lampridiformes (Regan, 1907). Several characters strongly support the assignment to the Trachipteridae, including (Olney, Johnson & Baldwin, 1993): absence of the supraoccipital crest, presence of first two dorsal-fin pterygiophores enlarged and inclined forward over the neurocranium, presence of a basisphenoid (Walters & Fitch, 1960), presence of lateral spinules on dorsal-fin rays (Olney, 1984), and presence of spines on lateral line scales. Also, the presence of stout pointed teeth in both jaws further confirm the species with the Trachipteridae (Palmer, 1986).

The family Trachipteridae consists of three genera (Fig. 7), *Desmodema*, *Trachipterus* and *Zu*, which clearly differ in general physiognomy (see, e.g. Fitch, 1964; Heemstra & Kannemeyer, 1984). Fishes of the genera *Desmodema* and *Zu* are characterized by the presence of abundant body scales (Walters & Fitch, 1960; Palmer, 1961), and the genus *Zu* can be distinguished by the presence of a small orbitosphenoid process (Oelschläger, 1983). The absence of an orbitosphenoid process and body scales therefore supports the inclusion of the new species in the



Figure 7. Cladogram summarizing Rosenblatt & Butler's (1977) proposal of interrelationships among Trachipteridae.



Figure 8. Comparison of the dorsal neurocranium bone arrangement in *Trachipterus mauritanicus* nov. sp. (a), *Trachipterus trachypterus* (b), and *Trachipterus articus* (c). (b) and (c) redrawn from Oelschläger (1983). Abbreviations: epo, epioccipital; pa, parietal; soc, supraoccipital.

genus *Trachipterus*. Although largely incomplete, the specimen can be easily assigned to a new species, especially by its neurocranial shape. The neurocranium of *Trachipterus mauritanicus* sp. nov. is more elongate and dorsally flattened with respect to that of its other congenerics (Regan, 1907; Oelschläger, 1983), and the dorsal portion of it has a characteristic arrangement of the bones (Fig. 8). As can be observed in Figure 8, the neurocranium of the other *Trachipterus* species, such

as Trachipterus articus and Trachipterus trachypterus, is deeper and shorter than that of Trachipterus mauritanicus sp. nov. The new species also differs from congenerics by the position of insertion of the dorsal fin. As described above, the dorsal fin of Trachipterus mauritanicus sp. nov. inserts at the level of the vertical through the midpoint of the orbit. The insertion of the dorsal fin is always situated well posterior to the orbit, at least behind the vertical through the posterior margin of the orbit in Trachipterus altivelis, Trachipterus arawatae and Trachipterus trachypterus (see, e.g. Walters & Fitch, 1960; Palmer, 1961; Nishimura, 1963; Fitch, 1964; Tortonese, 1970; Heemstra & Kannemeyer, 1986). A further character may be of relevance for evaluating the systematic placement of the new species: the presence of an endopterygoid ridge that extends onto the ectopterygoid and palatine. Such an endopterygoid ridge also is present in Radiicephalus elongatus (see fig. 11 in Olney, Johnson & Baldwin, 1993). Although additional more complete specimens are needed to improve our understanding of the relationships of Trachipterus mauritanicus sp. nov., it is interesting to note an high degree of resemblance, at least in its jaws and opercular bones morphology, to the extant Trachipterus arawatae (see May & Maxwell, 1986), a species that commonly occurs off South Africa (Heemstra & Kannemeyer, 1986), Australia (May & Maxwell, 1986), and New Zealand (Paulin et al., 1989).

## 5. Discussion

In his review of the fossil record of teleostean fishes, Patterson (1993) provided a scheme of the stratigraphic range of the Lampridiformes. The Trachipteridae were excluded in this scheme, as well as the Radiicephalidae, Regalecidae and Stylephoridae. Similar results were later discussed by Bannikov (1999), who listed fossil taxa belonging to this order. Although reported by neither of these authors, fossil remains assigned to the Trachipteridae were described by Bassani (1905) from the Pleistocene clay of Taranto, Apulia, southern Italy. This author described two largely incomplete specimens assigned to the species Trachipterus iris (= Trachipterus trachypterus). Unfortunately, these specimens were not figured and their description does not allow a precise taxonomic assessment. Bassani was dubious about the placement of the specimens, suggesting some affinities with the Regalecidae. The putative trachipterid material was lost and not reexamined in the later studies of the Taranto ichthyofauna (D'Erasmo, 1922; Montcharmont-Zei, 1957). However, the description of the two Pleistocene specimens from Taranto by Bassani (1905) contains no mention of features that could be interpreted as lampridiform and trachipterid synapomorphies as listed by Olney, Johnson & Baldwin (1993). For these reasons, Trachipterus mauritanicus sp. nov. should be considered as the first confirmed representative of the family Trachipteridae in the fossil record.

Taeniosomus lampridiforms are poorly represented in the fossil record. Members of the Radiicephalidae, Regalecidae and Stylephoridae are not known as fossils, whereas the Lophotidae are represented by at least three fossil genera. The earliest Lophotidae, Eolophotes lenis, was described by Daniltschenko (1962) from the Middle Eocene of Georgia. Arambourg (1943) described Lophotes elami based on two specimens, which are housed at the Laboratoire de Paléontologie of the MNHN in Paris, from the Oligocene deposits of Elam, Iran. This species was later reanalysed (Walters, 1957) and referred to the new genus Protolophotus (see also Arambourg, 1967). Oelschläger (1979) discussed the systematic status of the Iranian specimens and concluded that they belonged to separate taxa. He erected the new genus Protomecichthys for one of the specimens (the paratype MNHN EIP11), because of its resemblance to the extant lophotid genus Eumecichthys. However, he did not provide a formal diagnosis and description of the new taxon, thereby not fulfilling the requirements of the International Code of Zoological Nomenclature. Thus, as suggested by Bannikov (1999), the genus Protomecichthys is not valid. Examination of the Iranian specimens (MNHN EIP10; MNHN EIP11) revealed a clear taxonomic separation for the two fossil specimens. In agreement with the observations of Oelschläger (1979), one of the specimens (MNHN EIP11) shows strong similarities with the extant lophotid Eumecichthys. However, a more detailed morphological study of these fossils to elucidate their status is strongly recommended. An additional lophotid, Oligolophotes fragosus, was recently reported by Bannikov (1999) from the Lower Oligocene sediments of the Pshekha Formation, northern Caucasus.

Although rather rare, fossil bathysomous lampridiforms are characterized by an amazing disparity. The two living families, Lamprididae and Veliferidae, plus two exclusively extinct families, Palaeocentrotidae and Turkmenidae, and several taxa of difficult phylogenetic placement, are currently known as fossils. The Veliferidae are known from the Late Cretaceous (Campanian) from Nardò, Apulia, southern Italy (Sorbini & Sorbini, 1999), and another taxon, Veronavelifer sorbinii, was described by Bannikov (1990) from the Eocene of Monte Bolca, Italy. The only fossil Lamprididae, Lampris zatima, was described by various authors (Jordan & Gilbert, 1920; Jordan, 1925, 1927; David, 1943) from the Upper Miocene diatomites of Lompoc, California. The family Palaeocentrotidae was established by Bonde (1966) to accommodate Palaeocentrotus boeggildi from the Lower Eocene of the Fur Formation, Denmark (Kühne, 1941), originally described as a zeomorph. A brief description of an additional Palaeocentrotus specimen from the Lower Paleocene (Danian) of Denmark was

provided by Bonde (1992). The probably related genus Bathysoma was described by Davis (1890) from the Lower Paleocene (Danian) of Scania, southern Sweden. This genus has been assigned over many years to several perciform families (Woodward, 1901; Jordan, 1923; Romer, 1945; Bertin & Arambourg, 1958; Patterson, 1964), and later to the Lampridiformes (Patterson, 1968). Patterson (1968) considered it to be a member of the Veliferidae but he also noted its similarities to Palaeocentrotus. Slightly younger fragmentary Bathysoma specimens were recently collected in Sealand, Denmark, from erratic boulders of Late Paleocene age (Bonde, 1992). The family Turkmenidae comprises three genera, Analectis from the Upper Eocene and Lower Oligocene of the northern Caucasus (Daniltshenko, 1980; Bannikov & Parin, 1997), and Danatinia and Turkmene from the Upper Paleocene of Turkmenistan (Daniltshenko, 1968). Bannikov (1999) provided a detailed diagnosis of the family and genera. A further undescribed turkmenid taxon (aff. *Analectis*) was reported by Bonde (1987, 1997) from the Lower Eocene of Denmark. Bonde (1995) also reported a probable juvenile lampridiform from the same strata. An additional unusual fossil lampridiform, Bajaichthys elegans, was described by Sorbini & Bottura (1988) from the Eocene of Monte Bolca, Italy. This fish is known from a single juvenile individual, and it is probably a member of a new family. Finally, according to Bonde (1995), the genera Goniocranion and Whitephippus from the Eocene London Clay Formation (Casier, 1966) must be considered typical lampridiforms.

The origin of the Lampridiformes is not clear. Some Cretaceous fossils (Aipichthys, Araripichthys and Pharmacichthys) previously considered as related to this order (Rosen & Patterson, 1969; Silva Santos, 1985), are now placed within other euteleostean groups (see, e.g. Gayet, 1981; Maisey & Blum, 1991; Olney, Johnson & Baldwin, 1993; Otero & Gayet, 1995; Arratia & Chorn, 1998; Cavin, 2001; Maisey & Moody, 2001). The basal position of the Veliferidae is supported by the fossil record (see Sorbini & Sorbini, 1999). The Eocene occurrence of the Lophotidae implies that its sister taxa, Lamprididae, Stylephoridae, and Radiicephalidae, should have been present as well, suggesting a probable divergence of the two lampridiform lineages (Bathysomi and Taeniosomi) at least in the Paleocene. Also, the Miocene occurrence of trachipterids consequently suggests that their sister group, the Regalecidae, were already present at that time.

# 6. Conclusion

*Trachipterus mauritanicus* sp. nov. is the eighth member of the Messinian ichthyofauna from Sidi-Brahim. This ichthyofauna was described by Arambourg (1927), together with those from other localities of northwestern Algeria (Raz-el-Aïn, Les Planteurs, Gambetta, Saint Denis du Sig). Arambourg (1927, 1929) reported the presence of clupeids (Alosa elongata), sternoptychids (Argyopelecus logearti, Maurolicus muelleri), paralepidids (Paralepis albyi), myctophids (Hygophum probenoiti, Myctophum columnae) and bregmacerotids (Bregmaceros albyi) at Sidi-Brahim. Bregmacerotid skeletons were by far the most common elements of the fauna. The composition of the fauna clearly reflects the palaeoecological conditions of the depositional environment during diatomitic sedimentation. Arambourg (1927) interpreted the Sidi-Brahim ichthyofauna as a midwater assemblage. The occurrence of clupeids is restricted to a few scales found in the upper fossiliferous layers. The occurrence of a trachipterid in the diatomites of Sidi-Brahim is consistent with the ecological information furnished by other taxa (except Alosa elongata). Thus, like its other congenerics, Trachipterus mauritanicus sp. nov. was probably a mesopelagic fish.

After a cursory survey of the teleost fossil record, it is interesting to observe that to date, two families, Labrisomidae (*Labrisomus pronuchipinnis*) and Tripterygidae (*Tripterygion pronasus*), were known as fossils only from the Messinian deposits of the Oran region. In addition, these Algerian localities also provided the only fossil skeletal remains of the families Batrachoididae (*Halobatrachus didactylus*), Cepolidae (*Cepola cuneata*) and Pinguipedidae (*Parapercis mesogea*). The occurrence of the first fossil trachipterid in this area greatly reinforces the idea that the Miocene ichthyofaunas from the Oran region are of crucial importance for the fossil record of the Teleostei.

Acknowledgements. I wish to thank Walter Landini (Università di Pisa) and John E. Olney (Virginia Institute of Marine Science) for their suggestions and critical reviews of an early draft of the text. I am much indebted to Daniel Goujet (Muséum National d'Histoire Naturelle) for permission to examine the *Trachipterus mauritanicus* sp. nov. material. Thanks are also due to Federica Giudice for improvement of the English. Many thanks go to James C. Tyler (Smithsonian Institution), Niels Bonde (University of Copenhagen) and an anonymous reviewer for their helpful criticism on the manuscript. Niels Bonde kindly provided the Danish literature. This research was financially supported by the COLPARSYST funds of the Muséum National d'Histoire Naturelle, Paris.

#### References

- ARAMBOURG, C. 1927. Les Poissons Fossiles d'Oran. Matériaux pour la Carte géologique de l'Algérie, 1<sup>er</sup> Série-Paléontologie 6, 1–218.
- ARAMBOURG, C. 1929. Argyropelecus logearti, un nouveau Poisson bathypélagique du Sahélien. Bulletin de la Société Géologique de France 29, 11–15.
- ARAMBOURG, C. 1943. Note préliminaire sur quelques Poissons fossiles nouveaux. Bulletin de la Societé Géologique de France 43, 281–8.

- ARAMBOURG, C. 1967. Résultats scientifiques de la Mission C. Arambourg en Syrie et en Iran (1938–1939). II. Les poissons oligocenes de l'Iran. Notes et Mémoires sur le Moyen-Orient 8, 1–210.
- ARRATIA, G. & CHORN, J. 1998. A new primitive acanthomorph fish from the Greenhorn Formation (Late Cretaceous) of Nebraska. *Journal of Vertebrate Paleontology* 18, 301–14.
- BANNIKOV, A. F. 1990. An Eocene Veliferoid (Teleostei, Lampridiformes) from Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca* **6**, 161–74.
- BANNIKOV, A. F. 1999. A Review of Fossil Lampridiformes (Teleostei) Finds with a Description of a New Lophotidae Genus and Species from the Oligocene of the Northern Caucasus. *Paleontological Journal* 33, 68–76.
- BANNIKOV, A. F. & PARIN, N. N. 1997. The List of Marine Fishes From Cenozoic (Upper Paleocene–Middle Miocene) Localities in Southern European Countries. *Journal of Ichthyology* 37, 149–61.
- BASSANI, F. 1905. La Ittiofauna delle Argille Marnose Pleistoceniche di Taranto e di Nardò (Terra d'Otranto). Atti della Reale Accademia delle Scienze fisiche e matematiche di Napoli 12, 1–60.
- BERTIN, L. & ARAMBOURG, C. 1958. Super-ordre des Téléostéens. In *Traité de Zoologie*, tome 13 (ed. P.-P. Grassé), pp. 2204–500. Paris: Masson et Cie.
- BONDE, N. 1966. The fishes of the Mo-Clay Formation (Lower Eocene). *Meddelelser fra Dansk Geologisk Forening* **16**, 198–202.
- BONDE, N. 1987. *Moler Its Origin and Its Fossils, Especially Fishes.* Skamol: Nykøbing Mors, 53 pp.
- BONDE, N. 1992. Flint-fisk, moler-fisk, tropefisk og danekræ. VARV 1992, 35–41 [in Danish].
- BONDE, N. 1995. Tidligt tertiære fisk-flere danekræ. *VARV* **1995**, 24–30 [in Danish].
- BONDE, N. 1997. A distinctive fish fauna in the basal ash series of the Fur/Ølst Formation (U. Paleocene, Denmark). *Aarhus Geoscience* **6**, 33–48.
- CASIER, E. 1966. *Faune ichthyologique du London Clay.* London: British Museum (Natural History), 496 pp.
- CAVIN, L. 2001. Osteology and phylogenetic relationships of the teleost *Goulmimichthys arambourgi* Cavin, 1995, from the Upper Cretaceous of Goulmima, Morocco. *Eclogae geologicae Helvetiae* 94, 509–35.
- DANILTSHENKO, P. G. 1962. Fishes from the Dabakhan Formation of Georgia. *Paleontologicheskii Zhurnal* 1, 111–26 [in Russian].
- DANILTSHENKO, P. G. 1968. Fishes from the Upper Paleocene of Turkmenia. In Ocherki po filogenii i sistematike iskopayemykh ryb i beschelyustnykh (ed. D. V. Obruchev), pp. 113–56. Moscow: Nauka [in Russian].
- DANILTSHENKO, P. G. 1980. Order Lampridiformes. Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR 178, 91–6 [in Russian].
- DAVID, L. R. 1943. Miocene Fishes of Southern California. Geological Society of America Special Paper 43, 1–193.
- DAVIS, J. W. 1890. On the Fossil Fish of the Cretaceous Formations of Scandinavia. *Scientific Transactions of* the Royal Dublin Society (II) 4, 363–434.
- D'ERASMO, G. 1922. Contributo alla Ittiolitologia dell'Italia Meridionale. *Rendiconti della Reale Accademia delle Scienze Fisiche e Matematiche di Napoli* 28, 1–27.
- FITCH, J. E. 1964. The ribbonfishes (Family Trachipteridae) of the Eastern Pacific Ocean, with a description of a new species. *California Fish and Game* **50**, 228–40.

- FITCH, J. E. & LAVENBERG, R. J. 1968. Deep-water fishes of California. Berkeley: University of California Press, 155 pp.
- GAYET, M. 1981. Recherches sur l'ichthyofaune cénomanienne des Monts de Judée: Les "Acanthopterygiens". *Annales de Paléontologie (Vertébrés)* **66**, 75–128.
- GOÜAN, A. 1770. Historia piscium, sistens ipsorum anatomen externam, internam, atque genera in classes et ordines redacta. Strapsbpirg, 252 pp.
- GREENWOOD, P. H., ROSEN, D. E., WEITZMAN, S. H. & MYERS, G. S. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin* of the American Museum of Natural History 131, 339– 456.
- HAEDRICH, R. L. 1974. A rotating eye in *Trachipterus*. *Copeia* **1974**, 972–3.
- HEEMSTRA, P. C. & KANNEMEYER, S. X. 1984. The families Trachipteridae and Radiicephalidae (Pisces, Lampriformes) and a new species of *Zu* from South Africa. *Annals of the South African Museum* **94**, 13–39.
- HEEMSTRA, P. C. & KANNEMEYER, S. X. 1986. Trachipteridae. In *Smiths' sea fishes* (eds M. M. Smith and P. C. Heemstra), pp. 399–402. Berlin: Springer-Verlag.
- JOHNSON, G. D. & PATTERSON, C. 1993. Percomorph phylogeny: a Survey of Acanthomorphs and a New Proposal. *Bulletin of Marine Science* **52**, 554–626.
- JORDAN, D. S. 1923. A classification of fishes including families and genera as far as known. *Stanford University Publications, Biological Sciences* **3**, 77–243.
- JORDAN, D. S. 1925. The Fossil Fishes of the Miocene of California. Stanford University Publications, Biological Sciences 4, 1–51.
- JORDAN, D. S. 1927. The Fossil Fishes of the Miocene of Southern California. *Stanford University Publications*, *Biological Sciences* 5, 88–97.
- JORDAN, D. S. & GILBERT, J. Z. 1920. Fossil Fishes of the Diatom Beds of Lompoc, Californina. *Stanford University Publications*, 1–45.
- KRIJGSMAN, W., FORTUIN, A. R., HILGEN, F. J. & SIERRO, F. J. 2001. Astrochronology for the Messinian Sorbas basin (SE Spain) and orbital (precessional) forcing for evaporite cyclicity. *Sedimentary Geology* **140**, 43–60.
- KRIJGSMAN, W., HILGEN, F. J., LANGEREIS, C. G., SANTARELLI, A. & ZACHARIASSE, W. J. 1995. Late Miocene magnetostratigraphy, biostratigraphy and cyclostratigraphy in the Mediterranean. *Earth and Planet*ary Science Letters **136**, 475–94.
- KRIJGSMAN, W., HILGEN, F. J., RAFFI, I., SIERRO, F. J. & WILSON, D. S. 1999. Chronology, causes and progression of the Messinian Salinity Crisis. *Nature* 400, 652–5.
- KÜHNE, W. G. 1941. A New Zeomorph Fish from the Paleocene Moler of Denmark. *Annals and Magazine of Natural History* **7**, 375–86.
- MAISEY, J. G. & BLUM, S. 1991. Araripichthys SILVA SANTOS, 1985. In *Santana fossils. An illustrated Atlas* (ed. J. G. Maisey), pp. 208–17. Neptune City: t. f. h. Publications.
- MAISEY, J. G. & MOODY, J. M. 2001. A review of the problematic extinct teleost fish *Araripichthys*, with a description of a new species from the Lower Cretaceous of Venezuela. *American Museum Novitates* **3324**, 1–27.
- MANSOUR, B., MOISETTE, P., NOËL, D. & ROUCHY, J.-M. 1994. L'enregistrement par les associations de diatomées des environnements messiniens: l'exemple de la coupe de Sig (bassin du Chélif – Algerie). *Geobios* 28, 261–79.

- MAY, J. L. & MAXWELL, J. G. H. 1986. *Trawl fish from temperate waters of Australia*. Tasmania: CSIRO Division of Fisheries Research, 492 pp.
- MIYA, M., KAWAGUCHI, A. & NISHIDA, M. 2001. Mitogenomic Exploration of Higher Teleostean Phylogenies: A Case Study for Moderate-Scale Evolutionary Genomics with 38 Newly Determinated Complete Mitochondrial DNA Sequences. *Molecular Biology and Evolution* 18, 1993–2009.
- MIYA, M., TAKESHIMA, H., ENDO, H., ISHIGURO, N. B., INOUE, J. G., MUKAI, T., SATOH, T. P., YAMAGUCHI, M., KAWAGUCHI, A., MABUCHI, K., SHIRAI, S. M. & NISHIDA, M. 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 26, 121–38.
- MONTCHARMONT-ZEI, M. 1957. Ittioliti e foraminiferi delle argille pleistoceniche di Taranto. *Atti del Museo Civico di Storia Naturale di Trieste* **21**, 1–25.
- NISHIMURA, S. 1963. Observations on the dealfish, *Tra-chipterus ishikawai* Jordan & Snyder, with descriptions of its parasites. *Publications of the Seto Marine Biological Laboratory* **11**, 75–100.
- OELSCHLÄGER, H. A. 1976. On the evolution and ecological adaptations of the Allotriognathi. *Revue des Travaux de l'Istitute des Pêches Maritimes* **40**, 687–90.
- OELSCHLÄGER, H. A. 1979. Zur funktionellen Osteologie der Lophotidae (Pisces: Teleostei). Zoologische Jahrbücher 102, 336–60.
- OELSCHLÄGER, H. A. 1983. Vergleichende und funktionelle Anatomie der Allotriognathi (= Lampridiformes), ein Beitrag zur Evolutionsmorphologie der Knochenfische. *Abhandlungen der Senckenbergerichen Naturforschenden Gesellschaft* **541**, 1–127.
- OLNEY, J. E. 1984. Lampridiformes: development and relationships. In *Ontogeny and systematics of fishes* (eds H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall and S. L. Richardson), pp. 368–79. American Society of Ichthyology and Herpetology, Special Publication.
- OLNEY, J. E., JOHNSON, G. D. & BALDWIN, C. C. 1993. Phylogeny of Lampridiform Fishes. *Bulletin of Marine Science* 52, 137–68.
- OTERO, O. & GAYET, M. 1995. Étude phylogénétique des aipichthyides, poissons téléostéens de la Téthys cénomanienne. *Geobios M. S.* 19, 221–4.
- PALMER, G. 1961. The dealfishes (Trachipteridae) of the Mediterranean and north-east Atlantic. Bulletin of the British Museum (Natural History) Zoology 7, 335–52.
- PALMER, G. 1986. Trachipteridae. In *Fishes of the North*eastern Atlantic and the Mediterranean (eds P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese), pp. 729–32. Paris: Unesco.
- PATTERSON, C. 1964. A Review of Mesozoic Acanthopterygian Fishes, with Special Reference to Those of the English Chalk. *Philosophical Transactions of the Royal Society of London B* **739**, 213–482.
- PATTERSON, C. 1968. The caudal skeleton of Mesozoic acanthopterygian fishes. *Bulletin of the British Museum* (*Natural History*) Geology **17**, 47–102.
- PATTERSON, C. 1993. Osteichthyes: Teleostei. In *The Fossil Record 2* (ed. M. J. Benton), pp. 621–56. London: Chapman and Hall.
- PATTERSON, C. & ROSEN, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the

theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* **158**, 83–171.

- PAULIN, C., STEWART, A., ROBERTS, C. & MCMILLAN, P. 1989. New Zealand fish: a complete guide. National Museum of New Zealand Miscellaneous Series 19, 1– 279.
- POIGNANT, A. & MOISETTE, P. 1992. Foraminifères benthiques des intercalations marneuses d'une série diatomitique du Messinien d'Algerie. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 11, 667– 74.
- REGAN, C. T. 1907. On the Anatomy, Classification and Systematic Position of the Teleostean Fishes of the Suborder Allotriognathi. *Proceedings of the Zoological Society of London* 2, 634–43.
- REGAN, C. T. 1924. The morphology of a rare oceanic fish, *Stylephorus chordatus* Shaw; based on specimens collected in the Atlantic by the "Dana" expeditions, 1920–1922. *Proceedings of the Royal Society of London* 96, 193–207.
- ROMER, A. S. 1945. *Vertebrate palaeontology*. Chicago: University of Chicago Press, 687 pp.
- ROSEN, D. E. & PATTERSON, C.1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin* of the American Museum of Natural History **141**, 357–474.
- ROSENBLATT, R. H. & BUTLER, J. L. 1977. The ribbonfish genus *Desmodema*, with a description of a new species (Pisces, Trachipteridae). *Fishery Bulletin* 75, 843–55.
- SILVA SANTOS, R. D. A. 1985. Araripichthys castilhoi novo gênero e especie de Teleostei da Formação Santana, Chapada do Araripe, Brasil. Coletion de trabalhos de Paleontologia brasileira D. N. P. M. 1985, 133–9.

- SORBINI, C. & SORBINI, L. 1999. The Cretaceous Fishes of Nardò. 10°. Nardovelifer altipinnis, gen. et sp. nov. (Teleostei, Lampridiformes, Veliferidae). Studi e Ricerche sui Giacimenti Terziari di Bolca 8, 11–27.
- SORBINI, L. & BOTTURA, C. 1988. *Bajaichthys elegans*, an Eocene Lampridiform from Bolca (Italy). *Bollettino del Museo Civico di Storia Naturale di Verona* 14, 369–80.
- STIASSNY, M. L. J. & MOORE, J. 1992. A review of the pelvic girdle of acanthomorph fishes, with a provisional hypothesis of acanthomorph intrarelationships. *Zoological Journal of the Linnaean Society* **104**, 209–42.
- TORTONESE, E. 1970. Osteichthyes Pesci ossei. Fauna d'Italia X. Bologna: Edizioni Calderini, 556 pp.
- WALTERS, V. 1957. *Protolophotus*, a New Genus of Allotriognath Fish from the Oligocene of Iran. *Copeia* **1957**, 60–1.
- WALTERS, V. 1963. The trachipterid integument and an hypothesis on its hydrodynamic function. *Copeia* **1963**, 260–70.
- WALTERS, V. & FITCH, J. E. 1960. The families and genera of lampridiform (allotriognath) suborder Trachipteroidei. *California Fish and Game* 46, 441–51.
- WILEY, E. O., JOHNSON, G. D. & DIMMICK, W. W. 1998. The Phylogenetic Relationships of Lampridiform Fishes (Teleostei: Acanthomorpha), Based on a Total-Evidence Analysis of Morphological and Molecular Data. *Molecular Phylogenetics and Evolution* 10, 417– 25.
- WOODWARD, A. S. 1901. Catalogue of the fossil fishes in the British Museum (Natural History), IV. London: British Museum (Natural History), 636 pp.